SPATIAL DISTRIBUTION, MOVEMENT, AND GROWTH OF THE BULLFROG, *RANA CATESBEIANA* SHAW

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ABSTRACT

Populations of *Rana catesbeiana* in five ponds were observed for seven months in Williamsburg, Virginia. One population (pond A) was studied intensively, whereas the others were observed periodically. Altogether 183 bullfrogs were marked by toe-clipping of which 54% were recaptured. Other tagging methods included the use of waist bands and plastic discs attached to the dorsal skin. Bullfrogs from the other four ponds were introduced into pond A during late August and early September. Spatial distribution, movement, and growth were compared between the natives of pond A and the introduced bullfrogs.

Growth rates of native bullfrogs decreased with an increase in snout-vent length. There was no significant difference between growth rates of male and female residents. Introduced bullfrogs generally did not grow as well as the residents of pond A; in fact, some decreased in snout-vent length following their introduction. It is suggested that a behavioral interaction between native and foreign frogs accounted for decreased growth rates of foreign bullfrogs.

Both native and foreign bullfrogs preferred the same shoreline habitats. Four distinct habitats were defined according to the dominant vegetation. A ratio of percent observations of frogs to percent shoreline occupied by a vegetational habitat showed that the order of decreasing preference was: tree-shrub, cattail, tall grass, and short grass. When introduced into pond A, foreign frogs entered the habitats already occupied by natives; the short grass habitat remained virtually unoccupied. Nearest-neighbor distances did not differ before and after introduction of foreign bullfrogs. Thus, there appeared to be little or no effect of foreign frogs on spatial distribution of natives.

A new method is used to analyze the non-circular activity range of bullfrogs. Concentric probability rectangles which theoretically contained 68.3% and 95.4% of the bullfrogs' activity were calculated. Foreign frogs moved significantly less along the shoreline than natives. Movement towards and away from the water was essentially the same for native and foreign frogs. Within the native population, male frogs moved significantly farther along the shoreline than females. A statistical test also indicated that native females moved farther away from the shoreline than native males; however, this conclusion is judged biologically insignificant, since the actual difference in distance moved between the sexes was less than 0.5 meters. A model illustrating factors that influence movement of bullfrogs is proposed.

Homing behavior was observed in two adult male bullfrogs. Both were foreign frogs transferred to pond A from pond E, and both returned to within 25 meters of their original points of capture. They traveled overland distances of approximately 300-350 meters. Movement of bullfrogs between ponds occurred infrequently.

Breeding behavior differed between populations in two ponds. Male bullfrogs were arranged in a circle near the center of pond B and called in chorus, whereas males in pond A called only from the shoreline. Breeding behavior in the other ponds was not closely observed. Spawning occurred from May to late July; the peak of breeding occurred during late June.

Emergence of immature bullfrogs began in March followed by adults in April. The sex ratio was: 76 males, 68 females, and 39 immatures. Most bullfrogs disappeared by late October, although some adults were still active in early November.

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INTRODUCTION

Certain aspects of the life histories of ranid frogs have been extensively studied in North America and in Europe; some of the more important and well-known studies are mentioned here. Martof's studies of the green frog, *Rana clamitans*, have included territoriality (1953a), home range and movements (1953b), growth and development (1956a), and population structure (1956b). Hansen (1957) studied area of activity and growth of the river frog, *Rana heckscheri*. Heatwole (1961) reported on the habitat preference and activity of *Rana sylvatica*, the wood frog, during the non-breeding season. Turner (1960a) conducted a population study of the Western Spotted Frog, *Rana pretiosa*, wherein he emphasized the need for quantitative data of any anuran population, since ". . . our knowledge of vertebrate population ecology is based almost exclusively on studies of fish, birds and mammals." Savage (1961) has thoroughly studied the ecology and life history of the common frog, *Rana temporaria temporaria*. Whitaker (1961) discussed the habitats of *Rana pipiens* and *Rana clamitans* captured in various aquatic and terrestrial habitats. Oldham (1963) demonstrated homing behavior in *Rana temporaria* during its breeding time. Dole (1965a), during a study of movement of *Rana pipiens*, developed a trailing method that ". . . permitted a much more precise record of daily activity than has previously been possible with amphibians." Spatial distribution and homing in *R. pipiens* were also studied by Dole (1965b, 1968).

The bullfrog, *Rana catesbeiana*, has been the most frequently studied ranid. It naturally ranges east of the Rocky Mountains, from Canada to the Gulf of Mexico, but not into southern Florida (Wright and Wright, 1949). It has been introduced west of the Rocky Mountains (Wright and Wright, 1949) and into Puerto Rico (Perez, 1951) and Mexico.

General accounts of the life history of *Rana catesbeiana* have been reported by Dickerson (1931), Wright and Wright (1949), and Willis, Moyle, and Baskett (1956). Other reports have dealt with different aspects of bullfrog ecology. Homing behavior has been reported by McAtee (1921), Raney (1940), Ingram and Raney (1943), and Durham and Bennett (1963). Movement other than homing has been analyzed by Raney (1940), Ingram and Raney (1943), and Willis *et al*. (1956). Growth in bullfrogs from different areas of North America has been reported by George (in Turner, 1960b), Raney and Ingram (1941), Ryan (1953), Turner (1960b), Durham and Bennett (1963), and Schroeder and Baskett (1968). Diet has been studied by Frost (1935), Korschgen and Moyle (1955), Cohen and Howard (1958), Korschgen and Baskett (1963), and Brooks (1964). Age estimation and population structure were reported by Durham and Bennett (1963) and Schroeder and Baskett (1968). Studies of territoriality have been conducted by Emlen (1968a) and Wiewandt (1969). Vocalization has been studied by Frishkopf, Capranica, and Goldstein (1968), Capranica (1968), and Wiewandt (1969).

Although the ubiquitous bullfrog has been well studied, little is known of spatial distribution and areas of activity of individuals in their natural environment. Therefore, the purpose of this study was to analyze spatial distribution and range of movement of bullfrogs in a small pond. In addition, growth rates of a resident and an introduced population of bullfrogs were compared. Results from this seven-month study are compared with data from related studies.

STUDY AREA

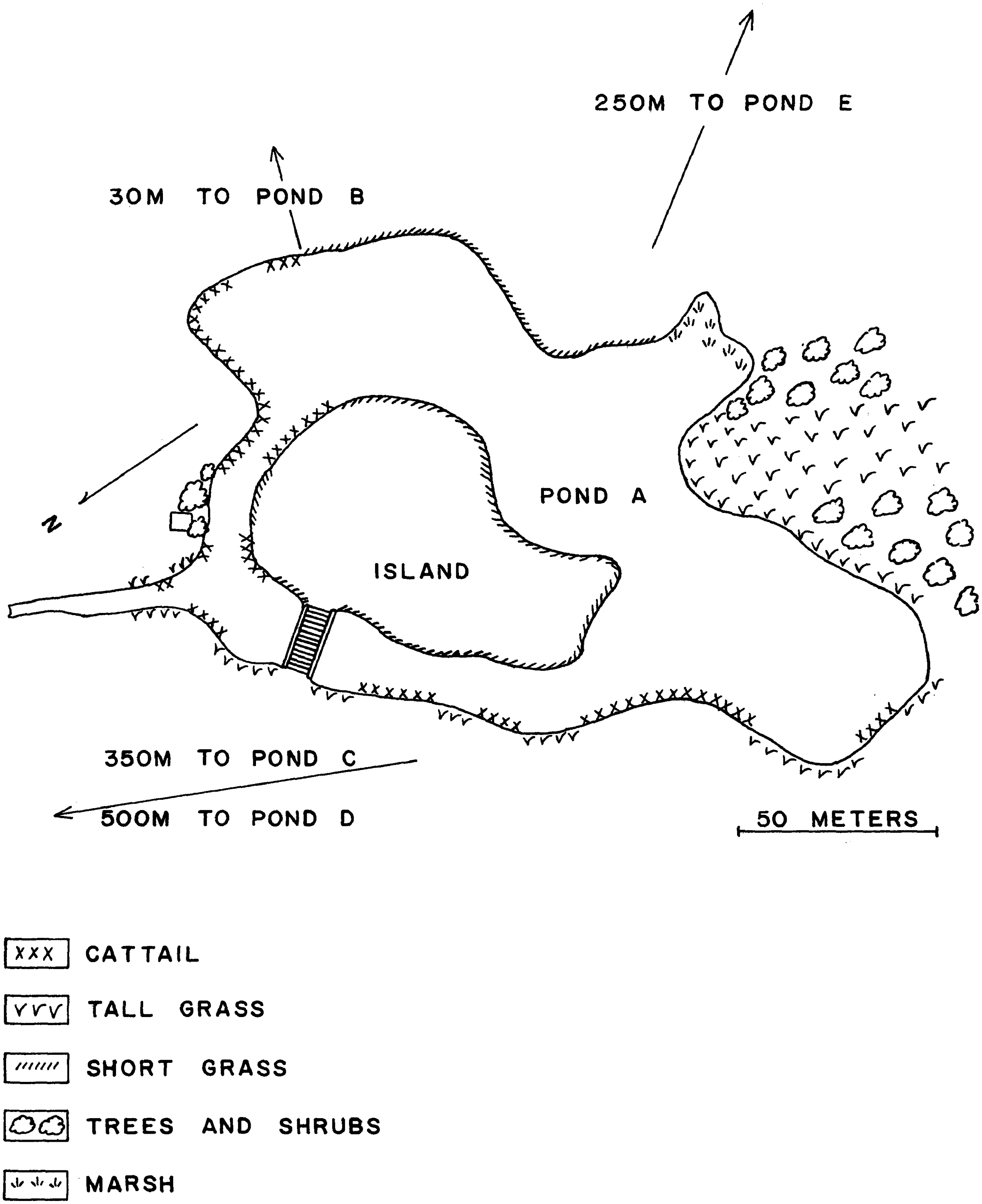
The study area consisted of five ponds located on the Golden Horseshoe Golf Course in Williamsburg, Virginia (Fig. 1). The data relating to spatial distribution, range of activity, and size of population were obtained from one pond, designated as pond A. The four other ponds, designated as B, C, D, and E, were primarily utilized as collecting areas from which bullfrogs were transferred to pond A. All ponds were used in observing bullfrog movement between ponds.

Pond A.--Pond A, the primary study area, supplied by underground pipes leading from B and C, had a surface area of approximately 2.3 acres and a maximum depth of 2 meters. A small island with a circumference of 150 meters and containing the 16th green was located near the east end. A footbridge connected the island with the north shoreline of the pond.

Broadleaved cattail (*Typha latifolia*), the dominant emergent plant, was located in shallow water except along the south and parts of the west shorelines. Interspersed among the cattails were lesser duckweed (*Lemna minor*) and water pennywort (*Hydrocotyle* sp.). Algae, particularly *Pithophora oedogonia*, were present usually in shallow water

Figure 1

Study area illustrating pond A and showing directions and distances to ponds B, C, D, and E.


250M TO POND E
30M TO POND B
N
POND A
ISLAND
350M TO POND C
500M TO POND D
50 METERS
CATTAIL
TALL GRASS
SHORT GRASS
TREES AND SHRUBS
MARSH

and periodically formed large floating mats on the water surface.

A weeping willow tree (*Salix babylonica*) and a large wax myrtle bush (*Myrica cerifera*) overhung a part of the east bank; this area was a preferred habitat for bullfrogs. A small cinderblock pump shed was located under the willow tree 2 meters from the shore. At the west end a wooded hillside was separated by a grassy area of the hill. This clear area served as a wide path leading from the top of the hill to pond A below. Hardwood flora on the hillside included white oak (*Quercus alba*), sycamore (*Platanus occidentalis*), northern red oak (*Quercus rubra*), yellow poplar (*Liriodendron tulipifera*), flowering dogwood (*Cornus florida*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), pawpaw (*Asimina triloba*), cottonwood (*Populus deltoides*), maple-leaved viburnum (*Viburnum acerifolium*), red mulberry (*Morus rubra*), black willow (*Salix nigra*), red maple (*Acer rubrum*), and black locust (*Robinia pseudoacacia*). The grassy area contained mainly *Agrostis alba* along with *Dactylus glomerata*, both of which overhung the waterline. Other plants interspersed along the shoreline included rushes (*Juncus* sp.), sedges (*Carex* sp.), mint (*Salvia lyrata*), lamb's lettuce (*Valerianella* sp.), jewelweed (*Impatiens* sp.), *Cornus stricta*, and a shadbush (*Amelanchier* sp.).

Pond B.--Pond B, located southeast of pond A, had a surface area of approximately 2.5 acres and a maximum depth of 2 meters. Ponds A and B were separated by a dam 30 meters wide, which included a narrow hard-surfaced roadway. Fed by an underground inlet, pond B was surrounded by cultivated turf, except at the extreme south end where it was bordered by hardwood. The shoreline vegetation was similar to that of pond A, with emergent cattail as the dominant plant.

Pond C.--Pond C, fed by D via an underground pipe, had a surface area of approximately 0.25 acre and a maximum depth of 2 meters. It was located about 350 meters northeast of pond A, and was separated from A by part of a fairway, a maintenance building, a small wooded area, and cultivated grass. A wooded hillside occupied the entire south side of C, while the remainder of the pond was surrounded by grass. There were no cattails around this pond.

Pond D.--Pond D, located in a completely open area 500 meters east of pond C, received water directly from the overflow of a smaller pond, and had a surface area of 0.5 acre and a maximum depth of 4 meters. A precipitous bank approximately 1.5 meters in height occupied most of the north side, and the remainder of the shoreline sloped gently.

Pond E.--Pond E was approximately 0.3 acre in surface area with a maximum depth of 2 meters. This pond, located in a ravine at a map distance of 250 meters southwest of pond A, was separated from pond A by a hill. Most of the south bank consisted of wooded hillside, with the remainder of the south shoreline bordered by cultivated grass. Tall grasses and weeds overhung the short east bank. Broad-leaved cattails dominated much of the north shoreline, with grasses and weeds on the sloped north bank. Cultivated grass covered most of the west bank.

Although the study area was located on a golf course, the ponds provided natural habitats for bullfrogs. Disturbance by golfers was considered minimal, since the data were obtained at night when the area was not used by golfers.

METHODS AND MATERIALS

Field work was conducted in 1968 from April, the time of emergence, to November, when the last bullfrogs hibernated. Prior to emergence, 49 wooden stakes were numbered with paint and placed 10 meters apart along the shoreline of pond A with the numbered ends 2-3 inches above the water surface. For each field trip the location of a captured or observed frog relative to a numbered stake was recorded to the nearest half meter on a map of pond A. The movements of each identified frog were also plotted on copies of the map.

All of the data were obtained from field work conducted primarily at night from 2130 to 0230 hrs, April through October. Occasional afternoon trips were made to all ponds for general observations. In searching for frogs at night, the usual procedure was to walk systematically along the shoreline, either in the water or on the bank, and to observe the water and adjacent land to a distance of approximately 10 meters from the shoreline. Due to overhanging vegetation and emergent cattails, wading was often necessary to observe frogs next to the bank or hidden in shallow water among the cattails. A hand lantern provided light.

During the very early part of the season, bullfrogs were captured by hand; however, they soon became increasingly difficult to capture because they would jump into the deep water when approached. A long-handled dip net was then tried, but did not result in an adequate increase in capture success, because the net was too shallow to hold frogs and the handle too heavy to allow quick thrusts. Then a lightweight insect net with a 3-foot handle was tried and did significantly improve capture efficiency. When a frog was observed in an area of dense vegetation, the net was placed at the location the frog would hopefully jump to after being disturbed. Some ingenious captures were performed using this method. Occasionally in confined areas, a frog was captured by hand.

Each bullfrog was marked for future identification by excising its toes with scissors, being careful not to injure the web between the toes. The following number scheme was used in marking. Units were indicated on the right hind foot, where a cut fifth phalanx stood for number one, a cut fourth phalanx for number two, etc. For units six through nine, combinations of two toes, the fifth and another, were used. Tens were indicated on the left hind foot, where a cut first phalanx stood for number ten, a cut second phalanx stood for number twenty, etc. Hundreds were indicated on the front feet. The fourth phalanx of the right foot stood for one hundred, and this was the only digit of the hundred series required in this study. No more than two toes were cut on one foot, and no more than five toes were cut on any frog.

Two other methods of tagging were also employed to help identify observed frogs that evaded capture. These methods had different degrees of success. The first is described as follows. A plastic red-orange disc, about 1.2 cm in diameter, was sewn onto the loose dorsal skin just over the clavicle of the bullfrog by the use of a suture needle and rayon bait-casting fishing line. The disc was actually a part of a Peterson fish tag manufactured by Floy Tag and Manufacturing, Inc. These discs, easily observed under lantern light, were applied to those frogs transferred from ponds C and D into pond A. Frogs from pond C had discs on the right shoulder, and those from pond D carried discs on the left shoulder. Although this method did not allow individual identification, it did permit me to distinguish transferred frogs from those which naturally inhabited pond A. In this study, native frogs were the natural inhabitants of pond A, and foreign frogs were those captured in neighboring ponds and transferred to pond A. Unfortunately, the success of the disc method was limited because the discs were lost within 2-3 weeks after application. Evidently, the thread slowly but progressively tore through the skin until the disc, with the thread attached, dropped off. The small wound healed quickly with no apparent harm resulting. Discs were not reapplied.

The second additional marking method, a banding technique first described by Emlen (1968b), proved relatively successful. Rayon elasticized bands were cut into lengths of 4-5 inches and were painted or marked with various color designs. The coloring schemes included orange and green luminous paint, and black and red waterproof ink. To add more colors, some white bands were dyed light green and some dyed orange. Foreign bullfrogs and those captured at pond A from early August to late September were marked with waistbands. A band was placed around the frog's waist to determine the proper size, i.e., one that would enable the band to stay on, but not be so tight as to interfere with normal activity. After obtaining the size, the band was removed from the waist, the ends stapled together, and slipped over the extended hind legs and around the waist. This method permitted accurate individual identification of banded frogs which were observed at a close distance, but evaded capture.

Several factors limited the effectiveness of the waistbanding method. Many bands eventually became muddy, obscuring the color pattern, thus making positive identification difficult. However, the muddy bands were replaced with new ones when the frogs were recaptured. A second factor involved the occurrence of open wounds which appeared between the bands and the ilia of those frogs that were bound too tightly. Whenever these wounds were discovered, the band was removed. On subsequent recaptures of these frogs, it was noted that the wounds healed well. A third, and less significant, factor involved the occasional loss of the waist band. In this case a new band was applied to the frog when recaptured. In spite of these limiting factors, use of the waist-band method was successful in that it enabled positive identification of bullfrogs that would not otherwise have been identified when observed.

Each time a frog was captured, its snout-vent length, sex, location, habitat, and body temperature were recorded in a small notebook. Data for each frog were later transferred to "Keysort" cards and also to a daily log. To measure a frog, a plastic rule was placed on the dorsal side of the outstretched frog, and the distance between the tip of the snout and the anterior lip of the cloaca was recorded in millimeters. This method proved to be somewhat imprecise; measurements of the same frog on two consecutive nights occasionally differed by as much as 4 mm.

The sex of mature bullfrogs (120 mm) was easily determined by tympanum size and ventral coloration. Tympanae of male frogs are noticeably larger than the eyes, and the venter is invariably yellow. In females, the tympanae are smaller than or only as large as their eyes, and the throat is usually white. Younger frogs (100-120 mm) were often more difficult to identify because sexual dimorphism was not as apparent as in older frogs. Bullfrogs less than 100 mm could not usually be identified according to sex.

Body temperature of bullfrogs was obtained by inserting a Schultheis thermometer into the cloaca for several seconds. Environmental conditions recorded for each trip included air temperature, water surface temperature, moon phase, cloud cover, visibility, and general descriptions of humidity and precipitation.

Foreign frogs were transferred from ponds B, C, D, and E to the island of pond A (Fig. 1). Before the transfer, most (28) foreign frogs were taken to the laboratory to be tagged and banded, where they remained in wet cloth sacks or in one-gallon containers for 1-3 days. Then they were released at night on the middle of the island of pond A and were permitted to disperse. The other six foreign bullfrogs were tagged, banded, and released on the island the same night they were captured. Table 1 summarizes transfer times of foreign frogs.

Periodically, ponds B, C, D, and E were searched to determine whether any foreign frogs had returned. Censusing of pond A revealed the differences in spatial distribution and movement between native and foreign bullfrogs.

Table 1

Transfer dates of foreign frogs to pond A

Date	Number of frogs transferred to pond A
31 Jul	5
21 Aug	3
5 Sep	18
9 Sep	2
11 Sep	6
Total	34

RESULTS AND DISCUSSION

Capture Success

Pond A was visited 75 nights, and the other four ponds were visited occasionally from April through September. From all five ponds a total of 183 bullfrogs were tagged, of which 98 were recaptured. However, 15 bullfrogs were tagged at different ponds after 28 September and therefore had little chance of being recaptured since the study was terminated soon after. Consequently, 168 bullfrogs was considered as the effective (recapturable) population when calculating recapture percentage. Table 2 summarizes the capture frequency data for pond A. Fifty-eight percent of the frogs in the effective population were recaptured, whereas the other 42% were captured only once.

Capture efficiency was calculated by dividing the number of frogs captured by the number observed. Using the dip net, the average capture efficiency was 33%. This efficiency increased significantly ($t = 4.033$; $P < .001$) to 59% after I began using the insect net (24 July) and the waist-banding technique (3 August). The insect net made it easier to capture frogs, while the banding method allowed identification of frogs seen but not captured. Frogs that were identified but not captured were counted as captured

Table 2

Recapture frequencies of native and foreign frogs at pond A

Number of times	Number of native frogs captured	Number of foreign frogs recaptured
0	--	11
1	59	11
2	33	2
3	23	2
4	9	2
5	3	3
6	3	1
7	1	0
8	0	1
9	2	1
10	1	0
Totals	134	34

Total of 365 captures at pond A.

when calculating efficiency.

It was generally noted that capture success was often correlated with habitat. Surprisingly, concealed bullfrogs and those found several meters from the water were the easiest to capture. Definitely, this appeared to be a behavioral characteristic. Perhaps a well-concealed and therefore rarely disturbed frog "sensed" security in immobility, a passive escape reaction. On the other hand, bullfrogs on land several meters from the water were readily visible and unprotected, and yet did not usually jump until after I placed the net over them. These frogs could not reach the water in a single jump and likewise may have "sensed" security in remaining stationary until physically disturbed. His initial leap would advertise his presence to a predator if the predator had not already noticed the frog. Therefore, if a frog distant from the pond were surprised by a predator (a light), immobility might have a greater survival value than an active escape reaction (jumping).

The most difficult frogs to capture were those located near the shoreline, either in shallow water or on land within 2 feet of the water. In this situation a frog would often dive or jump into the pond before I approached close enough to capture him.

Estimation of Population Size

It is difficult to obtain a true estimation of the size of a frog population. Existing methods and formulae for estimating numbers have been derived primarily from studies of higher vertebrates, and even these methods are criticized by those using them. In this study two methods were used to determine the population size at pond A. In the total count method, the largest number of bullfrogs observed during one night was used as the population size for that month. This total is assumed to be a slight underestimate because it is probable that every bullfrog was not observed on any one night.

A comparison was made between the total count and a modification of the "Lincoln Index" method described by Hayne (1949b). With Hayne's method the following formula gives the population number directly:

$$P = \frac{\Sigma WX^2}{\Sigma WXY}$$

where P = population size

W = number captured each trip

X = number previously handled

Y = proportion previously handled

The estimated population size is based on ". . . the increase in the proportion marked which is observed in succeeding catches, as more animals become marked. . . ." Two main assumptions must be made when using this method.

First, marked animals distribute randomly within the population, allowing both marked and unmarked animals equal probability of capture. Secondly, immigration and emigration will be insignificant between marking and sampling periods.

Data from all sampling periods at pond A were combined into six periods corresponding to the months April-September. Results of the two sampling methods are compared in Table 3. It is assumed that the total count provides a more accurate indication of population size than the method of Hayne (1949b). This assumption is made because I feel confident that most of the frogs were observed during each census. The 68 frogs calculated as the population size for April is an overestimate caused by the unusually large number of new frogs (19) captured on the night of 3 April. Comparisons of the two methods for the other five months are relatively close considering the small size of the bullfrog population at pond A. Newly metamorphosed frogs were not included in any population estimates; all other bullfrogs larger than 80 mm S-V-L were included in the estimates. Judging from the direct counts, it appears that no more than 30 native bullfrogs inhabited pond A at any one time.

Growth

There have been few studies on growth of the bullfrog under natural conditions. This may be due to

Table 3

Population estimates for pond A. All estimates include both native and foreign bullfrogs.

Month	Hayne estimate	Highest total count estimate	Average number of bullfrogs observed per census trip
Apr	68	26	20
May	30	19	15
Jun	36	25	19
Jul	15	19	17
Aug	10	20	12
Sep	24	23	16
Totals	183	132	
$\overline{X}$	30	22	

difficulty in recapturing individuals over a period of time. Raney and Ingram (1941) found considerable variation in growth rate of bullfrogs in Albany County, New York. Although immature frogs generally had a higher rate of growth than adults, some immature frogs grew slowly. Ryan (1953), who reported growth rates of bullfrogs in Ithaca, New York, did not find as much variation in the rate of growth of immature frogs. From emergence to the middle of May, little growth was evident among juveniles, whereas from the middle of May to September, the rate of growth was high. George (in Turner, 1960b) indicated that the growth rate of bullfrogs in Louisiana was greater than that of bullfrogs in New York. In Illinois, Durham and Bennett (1963) found that growth of individual bullfrogs varied considerably during a period of 1-3 years. In some frogs the growth rate was slow in one year and rapid in the next year, whereas other frogs steadily increased in size over the 3-year period. Bullfrogs from five different populations in Missouri had similar growth rates (Schroeder and Baskett, 1968); this was attributed to the similar feeding habits in bullfrogs of various habitats in Missouri (Korschgen and Baskett, 1963).

Growth of native bullfrogs in pond A

Growth data were obtained for 56 bullfrogs during one season of activity in pond A (see Appendix A for raw growth data). Individual frogs were captured two to five times, with the interval between captures ranging from 2 to 128 days. A typical growth pattern was obtained for the 44 native bullfrogs (Fig. 2). Slopes of the growth curves for immature and subadult frogs are generally steeper than for frogs over 130 mm. This indicates that bullfrogs less than 130 mm grew more quickly than those over 130 mm.

Further analysis of the growth data indicates the following: (1) frogs grew most rapidly in May and June (Table 4); (2) there was no significant difference ($t = 0.04$; $P > 0.5$) between growth rates of male and female bullfrogs; (3) an immature frog (60-75 mm) would normally grow 50 mm in 5 months, but a mature frog (120 mm) would increase by only 15 mm during the same period; and (4) only three immature frogs (26, 31, and 32) and one mature frog (123) showed no increase in growth.

<u>Growth of foreign bullfrogs in pond A</u>

Growth measurements were obtained from 12 foreign bullfrogs introduced into pond A at different times. In all, 34 frogs from neighboring ponds B, C, D, and E were transferred to pond A. Of the 12 frogs from which growth data were obtained, one was introduced in July, two in August, and nine early in September. These frogs grew at an average rate of only 1.5 mm per month compared to 4.0 mm per month, the average growth rate of 10 native frogs captured during the same period of time in pond A. Although there was no statistically significant difference ($t = 1.24$;

Figure 2

Growth curves of native and foreign bullfrogs.

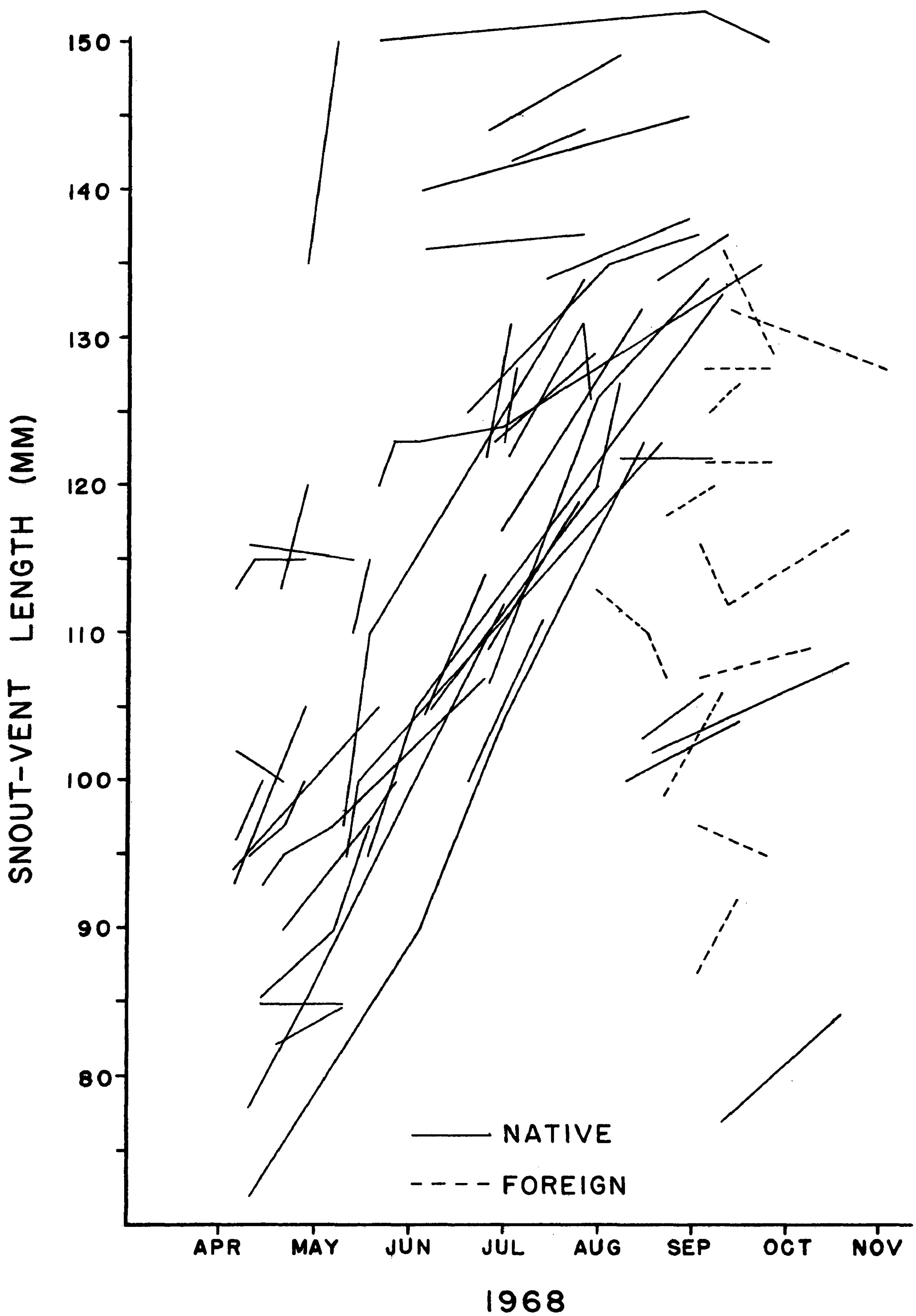

150
140
130
120
110
100
90
80
SNOUT-VENT LENGTH (MM)
NATIVE
FOREIGN
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
1968

Table 4

Average monthly growth rates of native bullfrogs in pond A. Growth rates were calculated from the growth curves in Figure 2.

Month	Average growth rate (mm/month)	N	S.E.	Range
Apr	6.4	14	1.48	-4.2 to 15.6
May	9.4	13	1.65	0 to 18.6
Jun	8.0	16	1.24	0 to 15.0
Jul	6.7	19	1.00	0 to 15.0
Aug	5.3	15	0.90	0 to 13.3
Sep	4.2	8	1.17	0 to 9.9

P > 0.2) between growth rates of native and foreign frogs, foreign frogs generally did not grow as well as natives. Six foreign frogs showed no increase in growth, and four of these actually showed a negative growth rate (Fig. 2). These four frogs decreased in snout-vent length over a period of 20-50 days (Appendix A).

According to Turner (1960b), "Apparent loss of length has been reported by almost all investigators of anuran growth." Different causes for anuran shrinkage have been postulated. Apparent loss in length in *Bufo terrestris americanus* has been reported by Raney and Lachner (1947), who felt that this loss was probably due to "unavoidable error in measuring live toads." Martof (1956a) reported a cessation and even loss of length in *Rana clamitans*. Martof suggested that as the frogs prepare for hibernation there may be a decrease in size if measurements are taken from snout to lip of cloaca. Ryan (1953) measured the length from snout to end of urostyle in three species of *Rana* and found no real loss of length. Turner (1960a) commonly found losses in mature male *Rana pretiosa*, and he stated that ". . . one might expect some 'shrinkage' of breeding males following nuptial activities." Standaert (1967) observed a loss of several millimeters in many carpenter frogs (*Rana virgatipes*) during a drought that drastically caused a reduction in the frogs' food supply. This decrease in length was attributed to lack of feeding along with increased catabolic metabolism caused by excessive temperatures.

In the present study, bullfrogs were measured from the tip of the snout to the anterior lip of the cloaca, and a real loss of length was detected in four foreign frogs. None of the native frogs during this same period of time showed a decrease in snout-vent length. It appears that loss of length of foreign frogs in pond A was not due to an error in measurement. It is suggested that the decreased and negative growth rates of foreign frogs resulted from a behavioral interaction between native and foreign frogs. In a new environment with unfamiliar neighboring frogs, foreign frogs may have responded by eating less than normally, thereby resulting in a decreased or negative growth rate. Experiments are currently being conducted to provide more conclusive evidence concerning loss of length in bullfrogs.

Spatial Distribution

Native bullfrogs

It is well known that most animals are not randomly distributed in nature, and the bullfrog is no exception. In this study, bullfrogs were found to prefer certain habitats along the shoreline of pond A. Four distinct habitats were defined according to the dominant vegetational type, and the percentage of total shoreline occupied by each type was calculated (Table 5). Only 7.8% of the total shoreline consisted of a combination of two or more types.

Table 5

Percentage of observations of native and foreign bullfrogs within various vegetational types around pond A

	Habitat				
	I Cattails	II Tall grass	III Short grass	IV Tree-shrub	V Other
% Shoreline occupied by habitat	28	26	34	4.5	7.5
% Observations of native frogs	53	22	3	19	3
% Observations of natives / % Shoreline occupied	1.89	0.85	0.09	4.22	0.40
% Observations of foreign frogs	61	4	7	28	--
% Observations of foreign frogs / % Shoreline occupied	2.18	0.15	0.20	6.22	--

Table 5 provides a summary of the habitat preferences. Fifty-three percent of all observations of natives in pond A were among cattails, which made up only 28% of the shoreline. Tall grass and the tree-shrub habitats contained approximately the same percentages of observations, but the latter vegetational type made up only 4.5% of the shoreline, whereas tall grass covered 26%. Although cattails contained the most observations, the most preferred habitat was type IV, trees and shrubs. This was determined by comparing the ratios of percent observations within a particular habitat to percent of shoreline occupied by the same habitat. The least preferred habitat was short grass, which contained only 3% of the observations, but occupied 34% of the total shoreline, resulting in a ratio of 0.09. It is assumed that open areas of cultivated grass did not provide sufficient cover and/or food, and were therefore virtually uninhabited by bullfrogs. It was generally observed that the more densely vegetated areas contained more insects and spiders than the open areas. In a comparative study of food habits of bullfrogs in Virginia, Brooks (1964) found insects and spiders to be the most important food items. Although predation of frogs was not considered in the present study, it was clear that vegetated areas of shoreline provided considerable cover from predators, whereas open areas provided no apparent cover. Availability of food and cover are probably the major factors affecting the general distribution of frogs in pond A.

Within dense vegetation, bullfrogs were normally located closer to each other than in less densely vegetated areas. There was usually vegetation or a topographic structure between any two frogs, which prevented closely aggregated frogs from viewing each other. Even in this situation frogs were rarely closer than 1 meter. Nearest-neighbor distances were determined for individual bullfrogs within the three preferred habitats for 16 nights prior to the transfer of foreign frogs to pond A. The average distances within habitats I, II, and IV were 8.1, 16.5, and 3.9 meters, respectively. Average nearest-neighbor distances correspond well with the summary of observations in Table 4 and indicate that the highest density of bullfrogs was in the trees and shrubs habitat, followed by decreasing densities in cattails, tall grass, and short grass.

Native and foreign bullfrogs

One objective of introducing foreign frogs to pond A was to determine whether the spatial distribution of native frogs would be altered. Another objective was to determine the subsequent distribution of foreign frogs within the pond. From a total of 34 foreign frogs introduced into pond A, 22 were later recaptured or observed within the various habitats. A chi-square test (Table 6) indicates that the five habitats were not occupied with the same relative frequencies by both native and foreign frogs ($\chi^2 = 15.7$; df = 4; $P < 0.01$). However, this conclusion

Table 6

2 x 5 Contingency table of number of observations at pond A classified by population (native and foreign) and habitat. Expected numbers of observations are in parentheses; observed numbers are above the expected.

Population	I Cattails	II Tall grass	III Short grass	IV Tree-shrub	V Other	Total
Native	338 (342)	143 (134)	17 (19)	118 (123)	21 (19)	637
Foreign	33 (29)	2 (11)	4 (2)	15 (10)	-- (2)	54
Total	371	145	21	133	21	691

$\chi^2 = 15.69$ $P < 0.01$

is misleading since the frequency difference between native and foreign frogs in the tall grass habitat contributed one-half of the chi-square value. Observations of native and foreign frogs did not differ significantly in habitats I, III, IV, and V. It was quite clear that foreign frogs occupied areas that were already inhabited by natives, and that foreign frogs did not inhabit the open short-grass habitat even though it was not occupied by other bullfrogs.

Both native and foreign frogs were observed with the same frequency at pond A during September, when most (26) of the foreign frogs were introduced. Average nearest-neighbor distances within three major vegetational types were calculated both before and after introduction of foreign frogs. A chi-square test (Table 7) indicates that spatial distribution did not differ significantly in the three habitats before and after introduction of foreign frogs ($\chi^2 = 0.97$). When determining nearest-neighbor distances, no distinctions were made in sex, size, or whether frogs were native or foreign.

Chi-square cannot properly be applied to distributions in which the frequency of any class is less than five. Although several expected frequencies are less than five for the tests illustrated in Tables 6 and 7, it is felt that chi-square does help to determine the spatial distribution of native and foreign frogs. Even though foreign frogs took up residence in the same habitats as the native frogs, there appeared to be no effect on spatial

Table 7

2 x 3 Contingency table of nearest-neighbor distance (m) classified by period of time (before and after introduction of foreign frogs) and habitat. Expected average distances (m) are in parentheses; observed average distances (m) are above the expected.

	Habitat			
Period	I Cattails	II Tall grass	IV Tree-shrub	Total
Before introduction of foreign frogs	8.1 (9.8)	16.6 (15.2)	3.9 (3.5)	28.5
After introduction of foreign frogs	11.4 (9.7)	13.5 (15.1)	3.1 (3.5)	28.3
Total	19.5	30.3	7.0	56.8

$\chi^2 = 0.966 \quad P > 0.50$

distribution of the population in pond A.

Within the different habitats, nearest-neighbor distances are probably affected also by social interactions associated with territoriality and social hierarchy. Martof (1953a), who studied spatial relationships of the green frog, Rana clamitans, observed that "when closely grouped, the frogs were spaced at surprisingly uniform distances of about two to three meters; however, a few were captured as close as 0.3 meter." He also found that breeding males maintained themselves in clusters and tended to remain in the same positions relative to each other within a cluster; they remained together even after moving overland to another body of water. Martof classified this social behavior as ". . . a primitive type of territoriality."

Although no distinctions of sex and size could be made in determining nearest-neighbor distances, one can speculate that a social organization exists among bullfrogs. If the spatial relationships of males remained relatively stable, a male could more easily recognize a female in his area. This would reduce aggression among males and would tend to increase reproductive success.

Movement

Range of movement within pond A

Burt (1943) defined an animal's home range as "the area about its established home which is traversed by the animal in its normal activities of food-gathering, mating, and caring for young." This concept was applied only to home ranges of mammals; the definition was inadequate for lower vertebrates, and it obviously excluded most invertebrates. Many lower vertebrates and invertebrates have certain breeding areas where they aggregate only for a very short time and only for the purpose of mating. It is also well known that these animals generally do not care for their young. Therefore, it seems that Burt's definition, although it may apply well to mammals, birds, and some insects, is not applicable to many animal species.

Dice (1952) defined home range as "the area over which an individual animal habitually travels while engaged in his usual daily activities," still including "all the feeding sites, breeding sites, and places of refuge habitually used by the individual. . . ." He also discussed the types and variation of home range, including seasonal variation. Little was known of amphibian home ranges at the time. More recently, Sanderson (1966) emphasized the ecological aspects of movement or home range rather than merely the plotting of various locations of animals. He stated that it must be determined ". . . why an animal is at a particular place at a particular time."

Using the definition of Burt or Dice, it would be difficult to establish a true home range for bullfrogs since it would obviously vary with the season. Only a comparative study of home range before, during, and after breeding would present a true ecological picture of home range. For example, during breeding, the males are virtually stationary while calling to females who move towards the males. Once a female approaches a male, she may mate with him or she may reject him and look for another male. Obviously, the range of movement of mature females will be larger than that of mature males during this time. Both before and after breeding, the ranges of both sexes may differ from their respective ranges during breeding. To complicate the ecological picture, juvenile frogs may exhibit a movement pattern different from adults at all seasons.

With the above considerations in mind, therefore, the term home range has not been used in this analysis of bullfrog movement since reproductive behavior and time of year were not considered. Movement was first analyzed by measuring the distance between the farthest two points of capture for each frog captured three or more times in pond A. This distance is commonly called the observed range length (Stickle, 1954). Table 8 presents average observed range lengths for each sex and both sexes together for native and foreign frogs at pond A. Observed range lengths of male and female natives do not differ significantly ($t = 1.49$; $P > 0.1$). However, native bullfrogs have a significantly ($t = 2.15$; $P < 0.05$) longer observed range length than foreign frogs. This method of analysis makes use of only two capture points for each animal and, therefore,

Table 8

Average observed range length for each sex and for both sexes together for native and foreign bullfrogs at pond A. Distances are expressed in meters.

	Native		Foreign		Native	Foreign
	♂	♀	♂	♀	♂ & ♀	♂ & ♀
Number of distances	46	39	24	15	85	39
Number of frogs	12	11	4	3	23	7
Average observed range length	18.2	11.0	5.1	4.7	14.7	4.9

does not truly characterize the areas of activity. The analyses presented below make use of all capture points and perhaps shed more light on the activity range of bull-frogs.

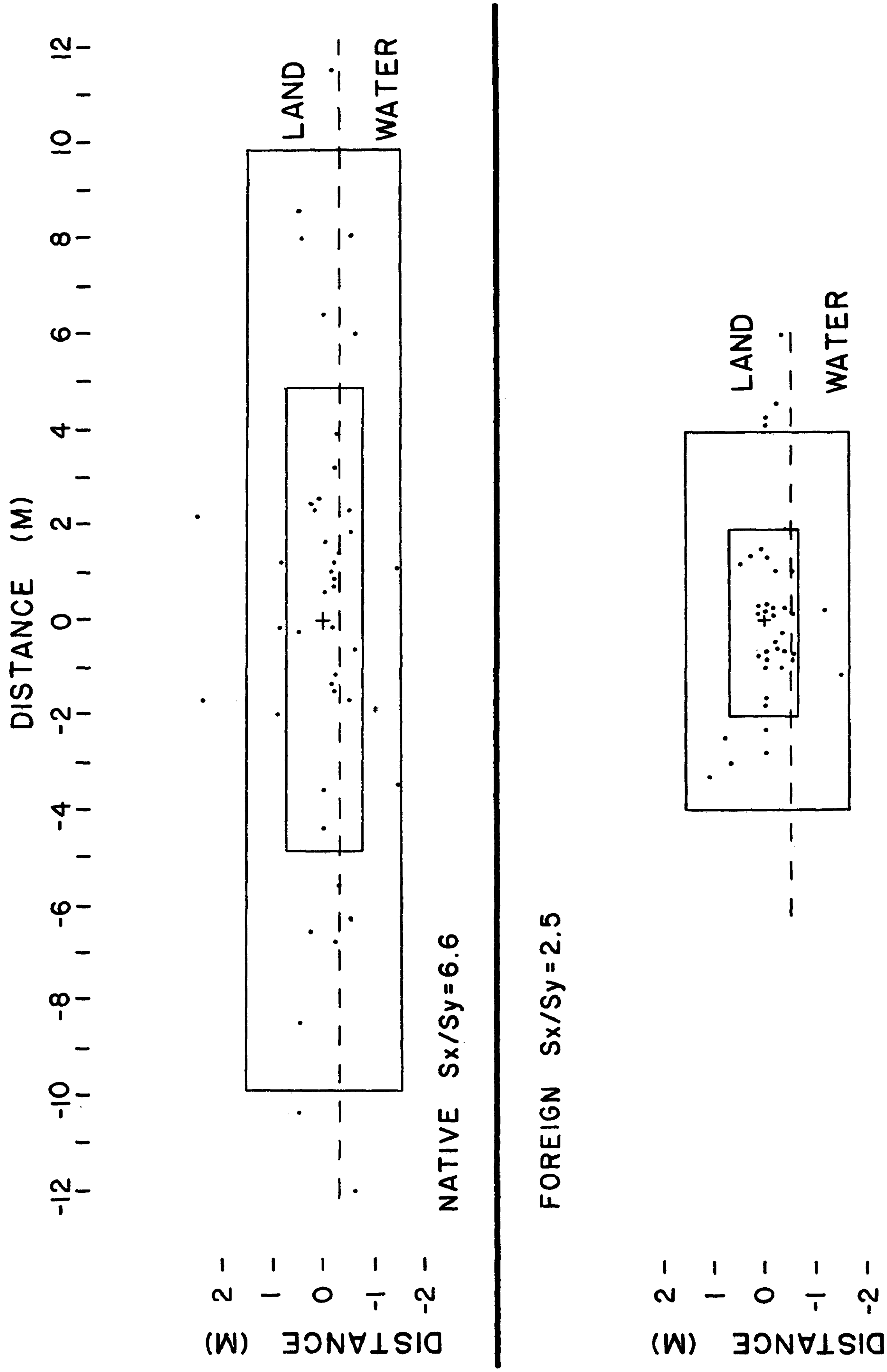
Many attempts have been made to determine the size and shape of an activity range for various animals. The results indicate these parameters to be quite variable among different groups. Size and shape depend on the physiological requirements and behavior of the animal along with the physical characteristics of the habitat. Harrison (1958) felt that an animal's home range ". . . could not be exactly delimited." Therefore, working with Malayan rats, Harrison calculated probability zones ". . . within which the rat spends varying proportions of its time." He deter-mined a standard diameter which was the diameter of the probability circle that contained 68.26% of the captures. Within this standard range (probability circle) an animal would theoretically spend 68.26% of its time. White (1964) discussed Harrison's concept of standard diameter and emphasized its usefulness as a comparative statistic both within and among population studies. White (1964), in a study of *Peromyscus leucopus*, found that males had larger ranges of activity than females, and that activity range decreased as population size increased. Both Harrison and White assumed activity ranges were circular. Stumpf and Mohr (1962) reviewed reports of linearity of activity ranges of various mammals, birds, and reptiles and indicated that oblong ranges were the rule in many cases. Their review further supports Sanderson's (1966) contention of a need for modification of our concepts of movement.

The composite range-map technique of Stumpf and Mohr (1962) and the statistical procedures described by Harrison (1958) and White (1964) have been combined to illustrate the non-circularity of bullfrog activity ranges and to contrast the movements of native and foreign bullfrogs. First, points of capture were plotted on graph paper, and the center of activity was calculated as described by Hayne (1949b) for each frog captured four or more times in pond A. Then an X-axis (designated the major axis) and a Y-axis (designated the minor axis) were drawn through the center of activity with the X-axis parallel to the shoreline. A transparent overlay graph was placed over each of the individual graphs in turn, and all points of capture were transposed onto a composite graph with a single center of activity and common Cartesian coordinate system (Fig. 3). A composite map was constructed for foreign frogs in the same manner (Fig. 3).

Difference in range of movement between native and foreign frogs was analyzed by modifying Harrison's concept of standard diameter to compensate for the non-circularity of bullfrog movement. The major modification was the construction of concentric probability rectangles analogous to probability circles of 1 and 2 standard diameters. The terms "standard major axis" and "standard minor axis" have

Figure 3

Composite map of capture points plus center of activity (+), shoreline (dashed line), and probability rectangles of one and two standard deviations for native and foreign bullfrogs. Sx = standard deviation of the distances between points of capture and the Y-axis; Sy = standard deviation of the distances between points of capture and the X-axis.


DISTANCE (M)
-12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12
LAND
WATER
NATIVE Sx/Sy=6.6
FOREIGN Sx/Sy=2.5
DISTANCE (M)
2 1 0 -1 -2

been used to define the "standard dimensions" of these probability rectangles.

Probability rectangles of 1 and 2 standard dimensions (1S and 2S probability rectangles) were obtained in the following manner. The standard deviation of the X-axis coordinates (Sx) of the 43 capture points for nine native frogs was calculated. The standard major axis of the 1S probability rectangle was calculated by doubling this standard deviation, i.e., 2Sx = 2(4.94) = 9.88 meters. Likewise, twice the standard deviation of the Y-axis coordinates (Sy) determined the standard minor axis of the 1S probability rectangle, i.e., 2Sy = 2(0.75) = 1.5 meters. Dimensions of the 2S probability rectangle are double those of the 1S rectangle. Dimensions for the 1S and 2S probability rectangles of the 39 capture points for seven foreign frogs were determined in the same manner.

Figure 3 shows center of activity, points of capture, position of shoreline, and 1S and 2S probability rectangles for native and foreign bullfrogs. Standard deviations and Sx/Sy ratios are presented in Table 9. Actual size of the 1S probability rectangle for native frogs is 9.9 x 1.5 meters, and that for foreign frogs is 4.0 x 1.6 meters. Fifty-three percent of the capture points of native frogs and 69% of the points of foreign frogs are within the respective rectangles. Position of the shoreline was obtained by averaging the distances from the center of activity for each frog to the actual

Table 9

Standard deviations of the X-axis and Y-axis distances to the center of activity for native and foreign bullfrogs and for the sexes of native bullfrogs at pond A. Standard deviations are in meters.

	Native	Foreign	Native	
	♂ & ♀	♂ & ♀	♂	♀
Number of frogs	9	7	11	12
Number of captures	43	39	42	44
Sx	4.94	2.02	8.98	5.20
Sy	0.75	0.80	0.48	0.90
Sx/Sy	6.58	2.52	18.71	5.78

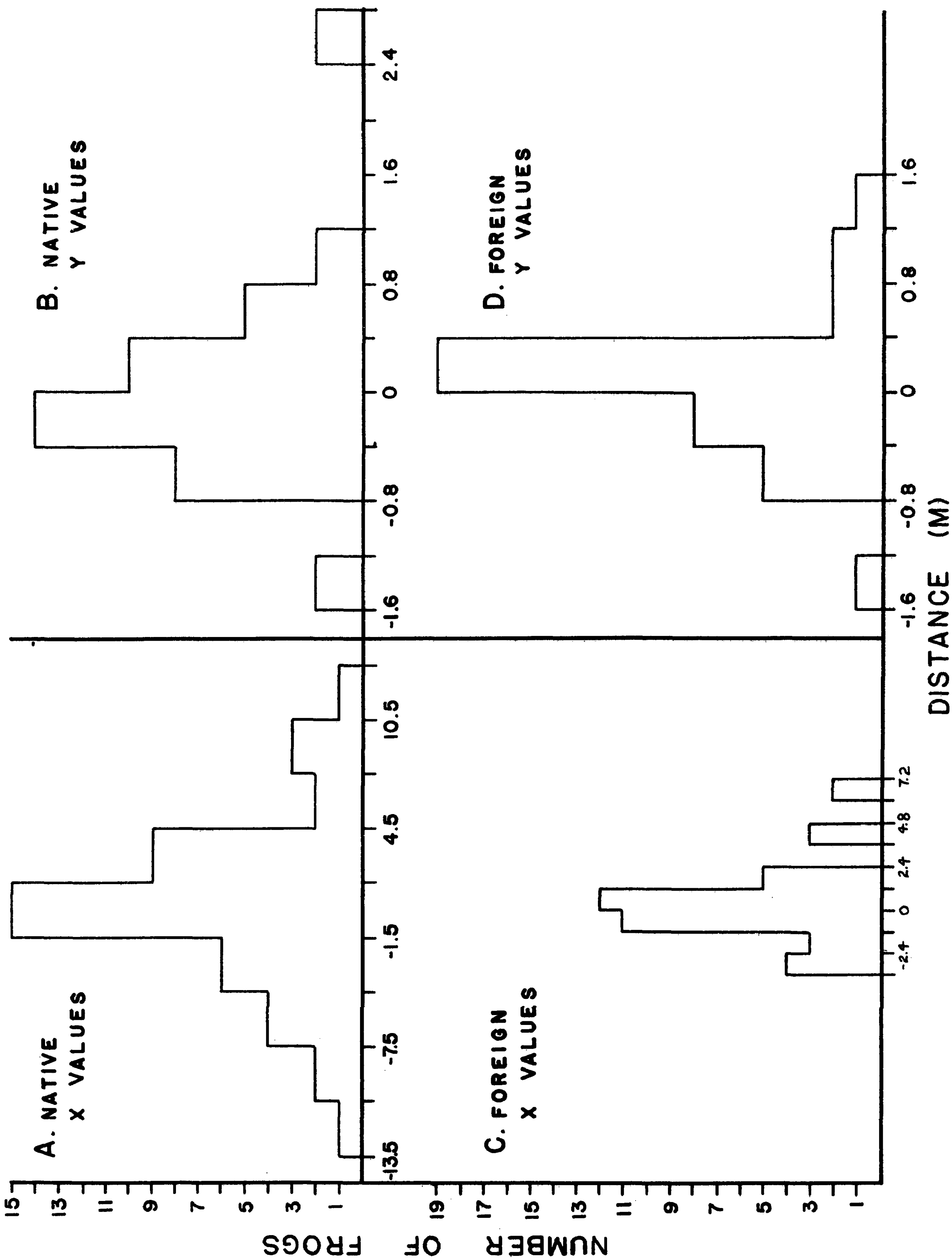
shoreline. The average distance between center of activity and shoreline is +0.3 meter for native frogs and +0.5 meter for foreign frogs.

Figure 4 illustrates frequency distributions of distances from capture points to the X-axis and to the Y-axis for native and foreign frogs. There is no theoretical reason to expect other than normal distributions for these four sets of data and, in fact, three of the four frequency distributions test as normal with a chi-square test at the 5% level. The y values for foreign frogs test as significantly non-normal due to the large number of observations in the 0 meter class.

Figures 3 and 4 both suggest that movement along the shoreline was less for foreign than native frogs and that movement towards and away from the water was about the same for these groups. The same two impressions are given in Table 9 by the Sx and Sy values for native and foreign frogs. The following statistical analysis was done to test these two impressions objectively. A test for equal variance of native and foreign x values indicated a significantly larger variance for the natives (S_x^2 for natives/S_x^2 for foreigns = $F = 6.00$; $P < 0.01$). This test is equivalent to comparing the dispersion of x values (about a common mean of 0 meter) in frequency distributions A and C of Figure 4. The test is also equivalent to testing the null hypothesis that Sx is the same for native and foreign frogs. The biological interpretation of the statistically

Figure 4

Frequency distribution of X-axis and Y-axis distances between points of capture and center of activity for native and foreign bullfrogs.


A. NATIVE X VALUES
B. NATIVE Y VALUES
C. FOREIGN X VALUES
D. FOREIGN Y VALUES
NUMBER OF FROGS
DISTANCE (M)
-13.5
-7.5
-1.5
4.5
10.5
-1.6
-0.8
0
0.8
1.6
2.4
-2.4
0
2.4
4.8
7.2
15
13
11
9
7
5
3
1
19
17
15
13
11
9
7
5
3
1

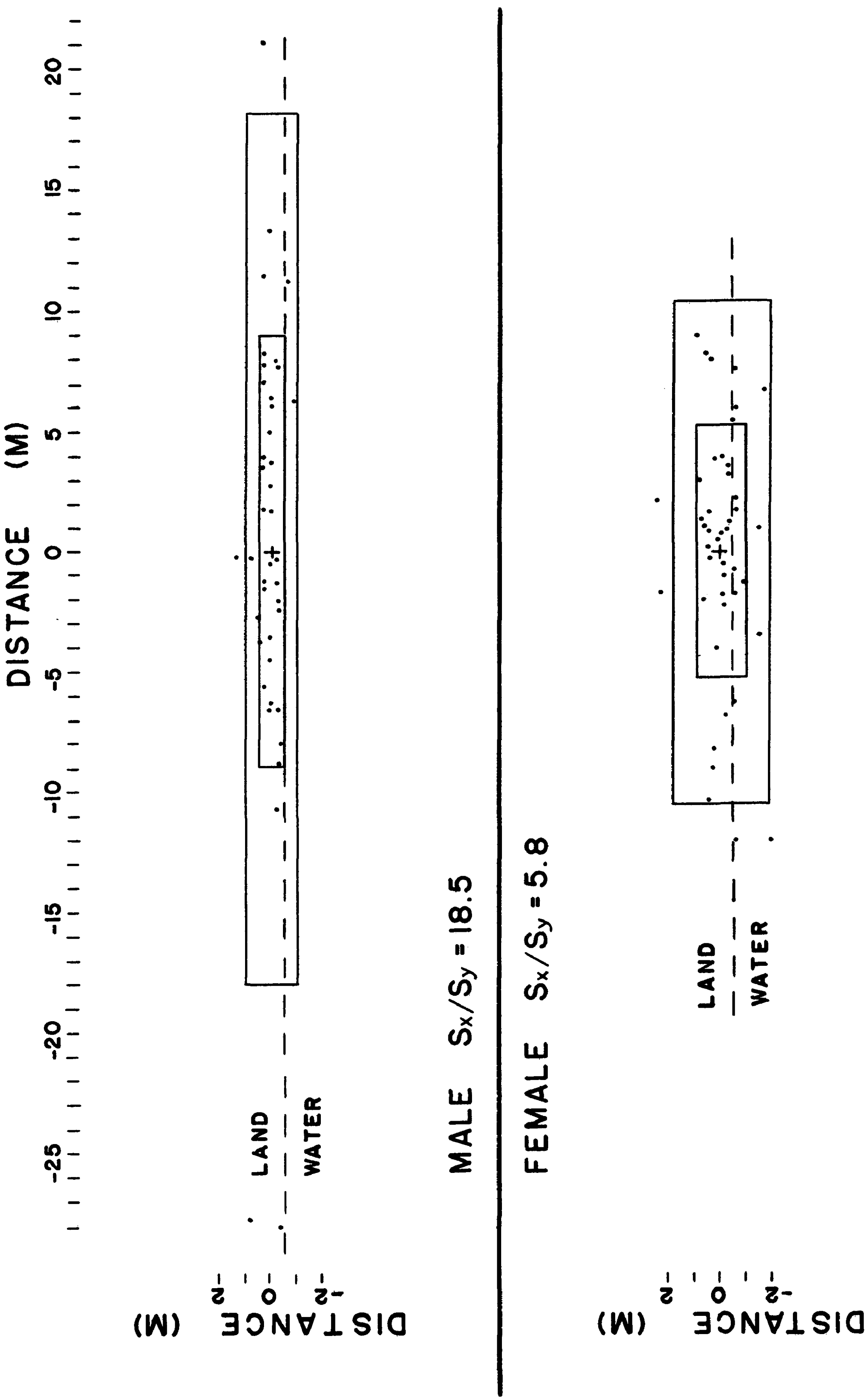
significant F value is that movement along the shoreline was less for foreign than native frogs. A similar F test revealed no difference between variances of native and foreign y values ($F = 1.14$; $P > 0.05$). This test is equivalent to comparing the dispersion of y values in frequency distributions B and D of Figure 4 and to testing the null hypothesis that Sy is the same for native and foreign frogs. The biological interpretation is that movement towards and away from the water was essentially the same for native and foreign frogs.

Movement data were similarly analyzed to show differences in movement between the sexes of 23 native frogs. In this analysis I used frogs captured three or more times in order to obtain a large enough sample. Standard dimensions of the 1S probability rectangle for males is 9.0 x 0.5 meters, and that for females is 5.2 x 0.9 meters (Fig. 5). Seventy-four percent of the capture points of native males and 59% of the points of native females are within the respective rectangles. The average distance between center of activity and shoreline is 0.5 meter for both male and female natives.

A test for equal variances of native male and female x values indicated a significantly larger variance for the males (S_x^2 for males/S_x^2 for females = $F = 2.98$; $P < 0.01$). This indicates that native males moved farther along the shoreline than females. A similar F test for y values revealed that the variance for females was

Figure 5

Composite map of capture points plus center of activity (+), shoreline (dashed line), and probability rectangles of one and two standard deviations for native male and female bullfrogs. Sx = standard deviation of the distances between points of capture and the Y-axis; Sy = standard deviation of the distances between points of capture and the X-axis.


DISTANCE (M)
-25
-20
-15
-10
-5
0
5
10
15
20
LAND
WATER
MALE $S_x/S_y = 18.5$
FEMALE $S_x/S_y = 5.8$
LAND
WATER
DISTANCE (M)
2
0
-2
DISTANCE (M)
2
0
-2

significantly greater than that of males ($F = 3.44$; $P < 0.01$). This test indicates that native females moved farther away from the shoreline than males. However, the actual difference between the standard minor axes of the male and female probability rectangles is only 0.4 meter. Therefore, I feel that there is no biological significance in the difference of movement away from the shoreline between native male and female bullfrogs.

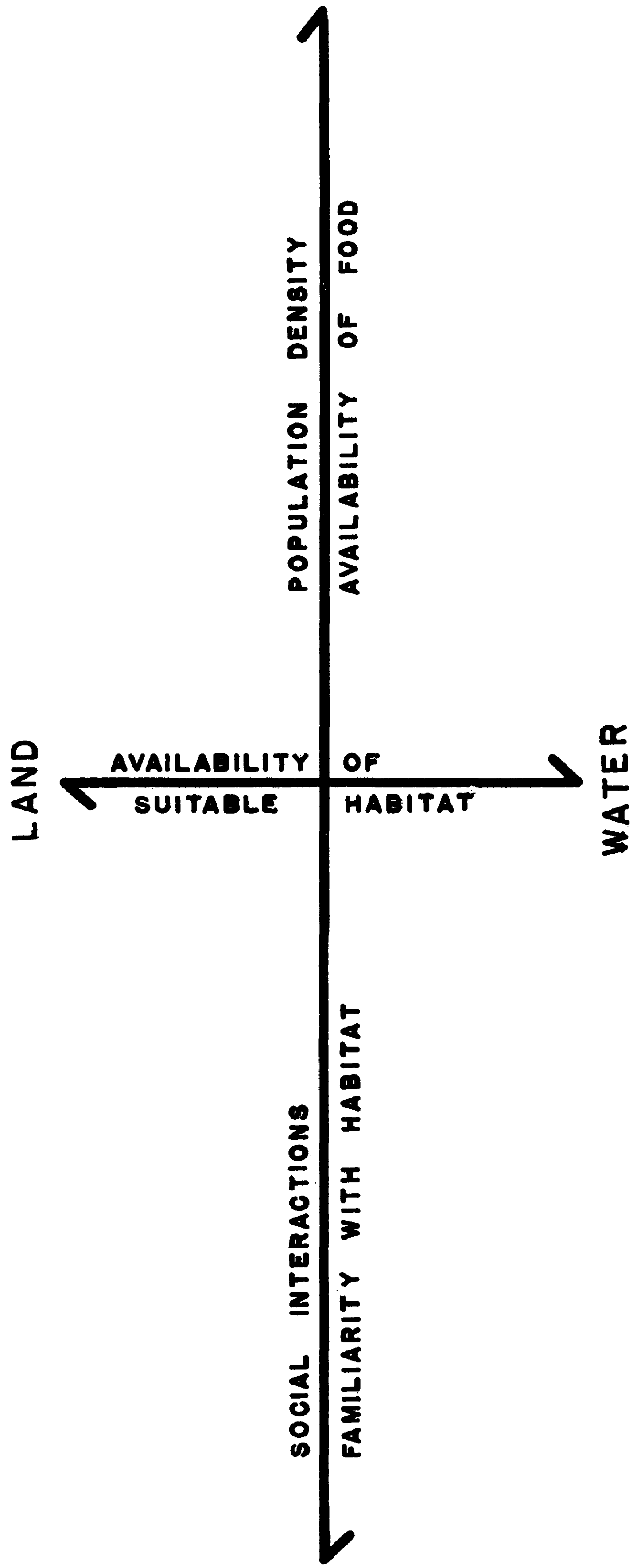
Range of movement is probably influenced both by biotic and physical factors of the environment, along with the behavioral characteristics and physiological requirements of the bullfrog. The above results indicate that the activity range of Rana catesbeiana is rectangular (or elliptical) in shape. Characterization of a rectangular activity range requires the estimation of two parameters, length and width. It is suggested that these two parameters are determined by two sets of at least partially independent factors. The following model is offered: the width of the rectangle, which is a measure of movement towards and away from the water, is determined primarily by availability of suitable habitat. A suitable habitat is an area located along the shoreline, in shallow water or on land, that provides vegetational and/or topographic concealment from predators. The length of the rectangle, which is a measure of movements along the shoreline--all in suitable habitat--is determined by a second set of factors, including social interactions, familiarity with habitat, population density, and availability of food (Fig. 6).

This model incorporates the two findings regarding the native and foreign frogs. First, the zone of suitable habitat was essentially the same for both groups of frogs and this is reflected by activity ranges of equal width. Second, the length of the activity range for foreign frogs is significantly less than that for native frogs. Assuming that all other factors influencing length of home range were equal, two explanations for the more restricted shoreline movement of the foreign frogs are: (1) lack of familiarity with the particular habitat, and (2) presence of native frogs in adjacent areas.

Perhaps the lesser movement of foreign bullfrogs found in this study is an indication of territorial behavior outside the breeding season. Emlen (1968a) defined territoriality as "the tendency for an animal to restrict its activities to a specified area and to defend this area against other members of its species." Durham and Bennett (1963) reported an apparent fight between two male bullfrogs lasting for ". . . at least one-half hour." Blair (1963) observed a contest between two male bullfrogs in which they ". . . butted, wrestled, shouldered each other around, [and] splashed a great deal. . . ." Both bullfrogs occasionally called during this 10-15-minute encounter. Emlen (1968a) demonstrated that male bullfrogs aggressively defend an area of water against other males

Figure 6

A model illustrating factors that influence movement of bullfrogs.


LAND
WATER
AVAILABILITY OF
SUITABLE HABITAT
POPULATION DENSITY
AVAILABILITY OF FOOD
SOCIAL INTERACTIONS
FAMILIARITY WITH HABITAT

during the breeding season. He suggested that a territorial male has a greater chance of mating than a non-territorial male. Capranica (1968), in studying the vocalization of bullfrogs in captivity, described three different types of calls, each associated with territorial behavior. One type was emitted by males only, a second by females only, and a third by both sexes. Wiewandt (1969) found a definite association between vocalization and territoriality in the bullfrog. Territorial males would attack a ceramic model of a bullfrog when the sound of a recorded "mating" call was emitted from a loudspeaker near the model. Males would always emit a distinctive vocalization in response to the recorded mating call. Two instances of fighting between male bullfrogs in a pond were also observed. Wiewandt (1969) pointed out that bullfrog territories were neither stationary nor clearly defined, and that the territorial limits may fluctuate ". . . when the male is at different locations within his territory."

In the present study, aggressive behavior among territorial native bullfrogs might have affected the activity ranges of foreign frogs. Activity ranges of native and foreign frogs have been found to overlap, but this is expected considering the habits and habitats of bullfrogs. For example, a "territorial" native frog in his isolated habitat may not initially detect another frog intruding into some part of his "territory." Consequently, the intruder (a foreign frog) may remain in this area until discovered by the native. Once detected, however, the foreign frog may have been attacked by the native bullfrog, and consequently chased from the latter's territory. This would tend to restrict or reduce the activity range of the foreign frog.

Another explanation for decreased movement among foreign frogs might be an avoidance behavior caused by their transfer to a different environment. Because of an unlearned behavior pattern (formerly called instinct), foreign frogs might respond by initially avoiding contact with "unknown" neighbors or by generally sensing security in minimum movement. Perhaps the combination of territoriality in natives and avoidance behavior in foreign bullfrogs accounted for the observed difference in movement and growth. I suspect that with time, movement ranges of foreign frogs would become similar in size to those of native frogs. Unfortunately, this study was not continued long enough to determine whether movement ranges increased, nor was it designed to study behavioral interactions among frogs.

Homing

Remarkably little evidence of homing in bullfrogs has been reported. McAtee (1921) described the homing behavior of one pet bullfrog. Raney (1940) transferred 31 bullfrogs (3 males, 1 female, and 27 immatures) from one pond to another pond 240 feet away. Two immature frogs returned to the home pond, but 17 others did not return; 12 were not recaptured. He felt that this evidence pointed to ". . . a lack of homing tendency in these bullfrogs." Ingram and Raney (1943) reported homing behavior of three bullfrogs which moved distances of 400, 570, and 675 feet to their respective home areas. Two of these moved overland and one probably traveled along a waterway. Durham and Bennett (1963) demonstrated "unmistakable homing behavior" in certain bullfrogs that returned to a specific section of shoreline after being released at another area in the same lake. They also reported other less well-defined evidence of homing in bullfrogs.

Homing behavior was not a major consideration during this study, but data from frogs 161 and 153 strongly support the existence of homing ability in bullfrogs. For the present study, homing was defined as the ability of a frog to return to the pond from which it was originally captured. Frogs 161 and 153 were both originally captured in pond E. Number 161, a male, was transferred to the island of pond A on the same night that he was removed from E. He was recaptured only twice--in pond A on 23 September and in pond E on 1 November, 24 meters from the original point of capture. A map distance between ponds A and E is 250 meters, but because there is a hill located between the two ponds, the overland distance is somewhat greater.

Data on frog 153, also a male, were more complete. On 5 September frog 153 was transferred from pond E to a small hill approximately 60 meters north of pond A. He was subsequently recaptured four times near cattails on the island of pond A. He was last observed in pond A on 23 September, and his absence was noted during the census on 28 September. On 29 September he was found back in pond E approximately 15 meters from the original capture site. It is interesting to speculate on when he returned to pond E, and what prompted the homing behavior at that time. There was no rainfall in Williamsburg from 10 to 26 September, and the average maximum and minimum temperatures were 27.5°C and 13.5°C, respectively. Then 0.36 inches of rain fell during a period from 1830 hrs on 26 September to 0200 hrs on 27 September. The next recorded rainfall was on 3 October. It is strongly suspected that frog 153 moved back to pond E during the rainy night of 26 September, and that the rain provided a cue. If this one well-documented instance is a real indication of homing behavior correlated with precipitation, rainfall should be considered in experiments on homing. Other bullfrogs also may have homed, but searching at other ponds was not intensive enough to verify this.

Dispersion

Unlike adult and subadult bullfrogs, newly metamorphosed bullfrogs did not appear to have any discernible pattern of movement other than dispersion. According to Howard (1960), "dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." In late June and in July, young frogs, many still with short tail remnants, were found dispersed in all directions from pond A. Even on dry nights they were as far as 75 meters from the water. Their movement seems to fit Howard's (1960) definition of dispersal, but no attempt was made to determine whether the movements were innate or environmental.

Before leaving the pond, these young frogs were commonly seen in aggregations along the shoreline. At pond A, I frequently observed groups of 5-10 newly transformed bullfrogs within a 1-square-foot area in shallow water or sitting on matted algae floating near the shore. They were also found along the south shoreline where older frogs were virtually absent. There was no apparent order in the spatial distribution of newly metamorphosed bullfrogs.

Breeding Observations

Calling

Breeding behavior differed in ponds A and B during the early part of the season. In pond B from 5 to 20 May, 10-15 male bullfrogs were observed sitting on matted algae about 15 meters from the shore. Arranged in a circular pattern, these bullfrogs regularly called in chorus for 5-10 seconds. One male would begin calling and a few seconds later others would join in. After 20 May the male chorus was not observed, and calling was heard only from isolated individuals along the shoreline.

In pond A bullfrogs were observed only near the shoreline. The first calls were heard on 6 April when the air and water temperatures were 6.5°C and 16.2°C, respectively. Only a few isolated calls were heard during each trip in April. By mid-May frogs were calling regularly around the shoreline, but not in chorus. Near the end of June, three or four isolated bullfrogs would regularly call in an apparent chorus. One frog would begin calling and the others would immediately join in; the chorus lasted for approximately 5 seconds. By the end of July calling was infrequent and sporadic. Weak-sounding, isolated calls were occasionally heard along the shoreline until the end of September.

<u>Time of breeding</u>

Time of breeding was determined by observance of egg masses. The first two bullfrog egg masses were observed on 3 June in pond B. Since pond B was not often studied during daylight hours, earlier egg masses may have been overlooked. The peak of the breeding season appeared to occur during the period of 18-30 June, when six egg masses were found in pond A. Amplexus was observed only twice. Egg masses were typically located in shallow water among emergent vegetation. Two other egg masses were found in pond A on 7 and 24 July. The duration of breeding was not determined; however, most of the spawning appears to have occurred from late May to early July.

Breeding observations from this study agree with those of Willis et al. (1956), who studied bullfrogs in Missouri. They determined time of breeding of Missouri bullfrogs by analyzing female gonads rather than relying on observation of egg masses. By calculating the percentages of spent ovaries during various time periods, they concluded that ". . . the peak of breeding occurred about the last week of June . . ." in two consecutive years. They also reviewed previous literature on bullfrog breeding, and then tabulated time of breeding for the bullfrog in various regions of the United States and Canada. In a later study of bullfrogs in Illinois, Durham and Bennett (1963) observed bullfrog egg masses ". . . during late May and early June of all years, and in most years the eggs had hatched by June 15."

Emergence, Sex Ratio, and Hibernation

Bullfrogs were first observed on 22 March when the air temperature was 17°C. Immature bullfrogs comprised 41% (16 frogs) of those tagged during April at pond A. During the next 5 months the ratio of mature to immature frogs was nine to one. It appears that immature frogs emerged earlier than the adult and subadult population.

The sex ratio for all tagged bullfrogs was: 76 males, 68 females, and 39 immatures. For bullfrogs tagged only at pond A, the sex ratio consisted of 49 males, 52 females, and 29 immatures.

By late October most of the adult bullfrogs at pond A had apparently hibernated. Only two mature bullfrogs were observed on 19 October. However, very small bullfrogs and some which had just metamorphosed were commonly observed during most of October. No frogs were observed at pond A on 25 October; the air and water temperatures were 14.5°C and 19.0°C, respectively.

In contrast to the absence of bullfrogs at pond A, there was considerable activity at pond E during late October. On 19 October, 17 bullfrogs were observed at pond E; at least 11 of these were known to be mature. Nine bullfrogs were observed on 25 October, but none were captured. On 1 November three mature bullfrogs were captured and one other mature frog observed at pond E; both air and water temperatures were 12.5°C.

There were no apparent reasons for the difference in activity of bullfrogs between ponds A and E. Air and water temperatures did not differ between the two ponds. Different geographical locations of the ponds may have contributed to the difference in activity, but this was not verified.

APPENDIX A

Growth data on *Rana catesbeiana*, Williamsburg, Virginia

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
2	♀	4 Apr	94			
		20 May	105	11	46	7.2
9	♀	4 Apr	96			
		13 Apr	100	4	9	13.3
10	♂	4 Apr	113			
		10 Apr	115	2	6	
		27 Apr	115	0	17	
				2	13	2.6
20	imm	4 Apr	93			
		27 Apr	105	12	23	15.7
26	♂	5 Apr	112			
		19 Apr	110	-2	14	- 4.3
28	♂	8 Apr	95			
		20 Apr	97	2	12	
		27 Apr	100	3	7	
				5	19	7.9
29	imm	8 Apr	78			
		27 Apr	85	7	19	
		30 Jun	112	27	64	
				34	83	12.3
30	♀	8 Apr	72			
		3 Jun	90	18	56	
		30 Jun	104	14	27	
		14 Aug	123	19	45	
				51	128	12.0

(continued)

APPENDIX A (continued)

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
31	♀	8 Apr	116			
		12 May	115	-1	34	- 0.9
32	imm	13 Apr	85			
		9 May	85	0	26	0
33	♂	13 Apr	93			
		20 Apr	95	2	7	
		6 May	97	2	16	
		24 Jun	107	10	49	
				14	72	5.8
35	♀	13 Apr	85			
		6 May	90	5	23	
		17 May	97	7	11	
				12	34	10.6
37*	♂	19 Apr	113			
		27 Apr	120	7	8	26.25
38	imm	19 Apr	82			
		9 May	85	3	20	4.5
41	♀	20 Apr	90			
		17 May	97	7	27	
		25 May	100	3	8	
				10	35	8.6
43*	♀	27 Apr	135			
		6 May	150	15	9	50.0
51	♂	9 May	95			
		12 May	100	5	3	
		20 Aug	123	23	100	
				28	103	8.2
52	♂	9 May	97			
		17 May	110	13	8	
		25 Jun	123	13	39	
		25 Jul	134	11	30	
				37	77	14.4

(continued)

APPENDIX A (continued)

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
53*	♀	12 May	110			
		17 May	115	5	5	30.0
60	♀	17 May	95			
		3 Jun	105	10	17	
		9 Sep	133	28	98	
				38	115	9.9
65	♀	20 May	150			
		3 Sep	152	2	106	
		23 Sep	150	-2	20	
				0	126	0
66	♂	20 May	120			
		25 May	123	3	5	
		3 Jun	123	0	9	
		30 Jun	124	1	27	
		23 Sep	135	11	85	
				15	126	3.6
74a	♀	3 Jun	140			
		3 Sep	145	5	92	1.6
74b	♂	5 Jun	105			
		31 Jul	120	15	56	
		6 Aug	127	7	6	
				22	62	10.6
75	♀	5 Jun	105			
		27 Jun	114	9	22	12.3
77	♀	5 Jun	136			
		25 Jul	137	1	50	0.6
81	♀	18 Jun	125			
		3 Aug	135	10	46	
		6 Sep	137	2	34	
				12	80	4.5
85	♀	18 Jun	100			
		12 Jul	111	11	24	13.7

(continued)

APPENDIX A (continued)

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
90	♂	24 Jun	107			
		31 Jul	126	19	37	
		9 Sep	134	8	40	
				27	77	10.5
91	♂	24 Jun	109			
		24 Jul	119	10	30	10.0
92*	♀	24 Jun	122			
		3 Jul	131	9	9	30.0
93	♀	25 Jun	123			
		31 Jul	129	6	36	4.9
97	♀	25 Jun	144			
		6 Aug	149	5	42	3.5
98*	♀	30 Jun	123			
		3 Jul	128	5	3	50.0
100	♂	30 Jun	117			
		29 Jul	127	10	29	
		13 Aug	132	5	15	
				15	44	10.2
102*	♂	2 Jul	122			
		25 Jul	131	9	23	
		29 Jul	126	-5	4	
				4	27	4.4
103	♂	3 Jul	142			
		25 Jul	144	2	22	2.7
107	♀	13 Jul	134			
		29 Aug	138	4	47	2.6
111	♀	24 Jul	134			
		16 Aug	137	3	23	3.9
119(f)	♂	29 Jul	113			
		16 Aug	110	-3	18	
		21 Aug	107	-3	5	
				-6	23	- 7.8

(continued)

APPENDIX A (continued)

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
123	♀	6 Aug	122			
		6 Sep	122	0	31	0
126	imm	14 Aug	103			
		3 Sep	106	3	20	4.5
128	imm	17 Aug	102			
		19 Oct	108	6	63	2.9
130	♂	9 Aug	100			
		14 Sep	104	4	36	3.3
131b(f)	♂	21 Aug	118			
		6 Sep	120	2	16	3.8
132(f)	imm	21 Aug	99			
		9 Sep	106	7	19	11.0
135(f)	♂	3 Sep	107			
		7 Oct	109	2	34	1.8
137(f)	♂	4 Sep	136			
		24 Sep	129	-7	20	-10.5
139(f)	♂	4 Sep	122			
		24 Sep	122	0	20	0
141(f)	♂	2 Sep	116			
		11 Sep	112	-4	9	
		19 Oct	117	5	38	
				1	47	0.6
143(f)	imm	2 Sep	87			
		14 Sep	92	5	12	12.5
145(f)	♀	2 Sep	128			
		24 Sep	128	0	22	0
148(f)	imm	2 Sep	97			
		24 Sep	95	-2	22	- 2.7
153(f)	♂	5 Sep	125			
		14 Sep	127	2	9	6.7

(continued)

APPENDIX A (continued)

Frog number	Sex	Date captured	S-V-L (mm)	Increase in S-V-L	Days elapsed	Rate of growth (mm/month)
157	imm	9 Sep	77			
		16 Oct	84	7	37	5.7
161(f)	♂	11 Sep	132			
		1 Nov	128	-4	51	- 2.3

*Apparent error in measurement.

(f) = Foreign bullfrogs.

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